The Veliger 39(1):71-82 (January 2, 1996)

# A New Species of Eastern Pacific Fissidentalium (Mollusca: Scaphopoda)

by

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#### AND

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Abstract. Fissidentalium erosum sp. nov. is described morphometrically from specimens collected from deep water off California. It is distinguished from F. megathyris primarily on the basis of softbody-part proportions and radular characteristics. Shell differences are slight; the ventral aperture of F. erosum is approximately circular, whereas in F. megathyris the aperture is distinctly wider than high. The posterior portion of Fissidentalium erosum shells is often eroded, in contrast to the uneroded condition of most F. megathyris shells collected at the same station.

## INTRODUCTION

During an examination of 38 scaphopod specimens collected from one station and tentatively identified as *Fis-sidentalium megathyris* Dall, 1890, 19 were noted to have a series of slight, but consistent differences from the other "typical" *F. megathyris*. In addition to minor differences in the shell, these specimens had evident and statistically significant differences in many soft body parts and radular characteristics.

Fissidentalium megathyris was originally described from specimens collected near the Galapagos Islands from depths greater than 1000 m (Dall 1890). Subsequent collections have generally confirmed that this species is characteristically collected at depths from about 1000 to 2500 m (Pilsbry & Sharp 1897). Fissidentalium megathyris is a large scaphopod, probably the largest in waters adjacent to North America. Large animals are relatively uncommon in collections, and unlikely to be examined as quantitatively as were the ones in our samples.

The first of the two groups found in this study closely matched the description of *F. megathyris*. The shells of the second group were consistently highly eroded and often stained with a tightly adherent black material which made those shells visually distinct from the uneroded, "typical" *F. megathyris.* These differences indicate that the two groups of specimens likely occupy two distinct habitats, with differing sediment chemical characteristics. Given that the two groups have consistent differences of shape, and in radular and soft-body-part proportions, and given that they likely occupy two chemically distinctive habitats, we think that both groups warrant species status and name the second taxon *Fissidentalium erosum* herein.

Sea anemones (of a currently undescribed species; D. Fautin, personal communication) were found on some of the *F. megathyris* shells, but never on *F. erosum* shells. It is possible that *F. erosum* may live deeply buried in the sediment, whereas *F. megathyris* may live very near the sediment surface. This relationship with the sea anemone appears to be opportunistic rather than species-specific; specimens of another deep-water scaphopod from south-central California are also found carrying sea anemones that appear to be the same species (Shimek, in preparation).

# MATERIALS AND METHODS

Specimens examined for both descriptive and comparative purposes came from the collections of the Moss Landing

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# Table 1

Specimens examined. For museum lots with more than one specimen, we designated the specimens. For the Moss Landing Marine Laboratories (MLML) specimens, the designations were FM1-FM22 and NS1-NS19. For all other specimens, the designations were alphabetic, in order, starting with A in each new lot number. Type specimens are noted, but these data were taken from specimen label information. Station data for FM20-FM22 from Nybakken, et al., 1992.

S	pecimen				
Species	Designation	Lot		Ν	Comments
A. Fissidentalium megathyris	FM1-FM15	Р3	MLML	15	Station P3, Collected with: Beam Trawl. 37°03.27'N, 123°26.30'W (on bottom) to 37°03.97'N, 123°25.26'W (off bottom). 29 February 1992. Depth = 3090- 3300 m.
	FM16-FM19	M4	MLML	4	Station M4, Collected with: Beam Trawl. 36°20.30'N, 122°36.44'W (on bottom) to 36°19.77'N, 122°35.71'W (off bottom). 1 March 1992. Depth = 2630- 2790 m.
	FM20-FM22	LIIT14	MLML	3	Station LIIT14, Collected with: Beam Trawl. 37°35.0'N, 123°30.1'N (on bottom) to 37°35.0'N, 123°28.8'N (off bot- tom). 30 July 1991. Depth = 3015-2690 m.
	A-B	085479	CAS	2	Off Santa Barbara.
		87558	USNM	1	Station 2789; 1342 fm. (2446 m), Off Chiloe Is.
		594262	USNM	1	Station 2807; 812 fm. (1496 m) "Lectotype".
	A–J	265901	USNM	10	Station 5673; 1090 fm. (1195 m), 31°26'N, 117°42'W.
	A-R	95851	USNM	18	Station 2807; Specimen A = "Fig- ure Type".
	A-W	266823	USNM	23	Station 5693; 868 fm. (1588 m). S.W. of San Diego.
B. Fissidentalium erosum	NS1-NS19	Р3	MLML	19	Station P3, Pioneer Canyon, 3090- 3300 m. (See above.)

Marine Laboratories (MLML). Additional specimens of nominal *F. megathyris*, for comparative purposes, were loaned from the California Academy of Sciences, San Francisco (CAS) and the National Museum of Natural History, Washington (USNM) (Table 1). Type specimens designated in this paper were deposited in the Los Angeles County Natural History Museum (LACM); United States Natural History Museum; and the British Natural History Museum (BMNH).

## Shell Measurements and Morphometrics

Shell measurements were made following Shimek (1989), with the following changes (Figure 1). Shimek's (1989) measurement of Aperture Width is actually a measure of Aperture Height. The measure of Aperture Height in this study is the same as that measure designated Aperture Width in the earlier study (Shimek 1989). Aperture Width in this study refers to the maximum apertural distance between the two lateral sides of the shell.

For the shell description, we used an approach of quantitative shell morphometric analyses based on the mathematical properties of shell shape (Raup 1966). The morphometric analyses ideally require "perfect" undamaged shells. Such shells are rare, and to increase statistical reliability, we found it necessary to examine and measure shells with minor fractures, apertural lip breaks, and apical fractures. We tried to be as conservative as possible in the use of these shells, but their use undoubtedly increased variance in the analyses. For detailed derivations of the indices and measurements, see Shimek (1989).

Only 14 of the *F. erosum* specimens had intact shells which were used for shell comparisons. Most of the museum specimens were from distant localities; for example, the type locality for *F. megathyris* is the Galapagos Islands (Dall 1890). Given that scaphopods develop from demersal

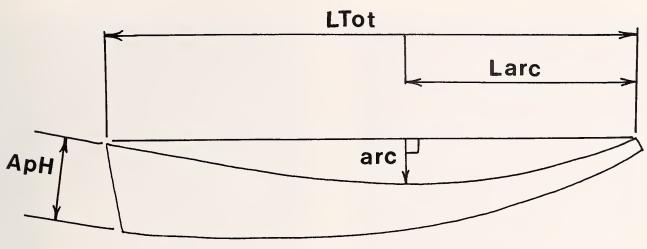


Figure 1.

Shell measurements of all specimens; all orientations labeled anatomically, i.e., the foot is ventral. Abbreviations: ApH = interior height of the ventral aperture, measured perpendicular to the anteriormost shell surface; arc = maximum perpendicular distance from a line connecting the anteriormost margin of the dorsal aperture to the anteriormost margin of the ventral aperture; Larc = distance from the anteriormost margin of the dorsal aperture to the point where measurement "arc" was taken; LTot = total length, from anteriormost margin of the dorsal aperture to the anteriormost margin of the ventral aperture. Measurement ApW (not shown) is taken perpendicular to measurement ApH across the widest part of the ventral aperture.

larvae, with short planktonic periods (Shimek & Steiner, in press), we thought local and distant populations of individuals assigned to F. megathyris might have different characteristics. Consequently, where possible, data from F. erosum were compared to the data from the total F.megathyris data set and to those data obtained from the nearby California populations.

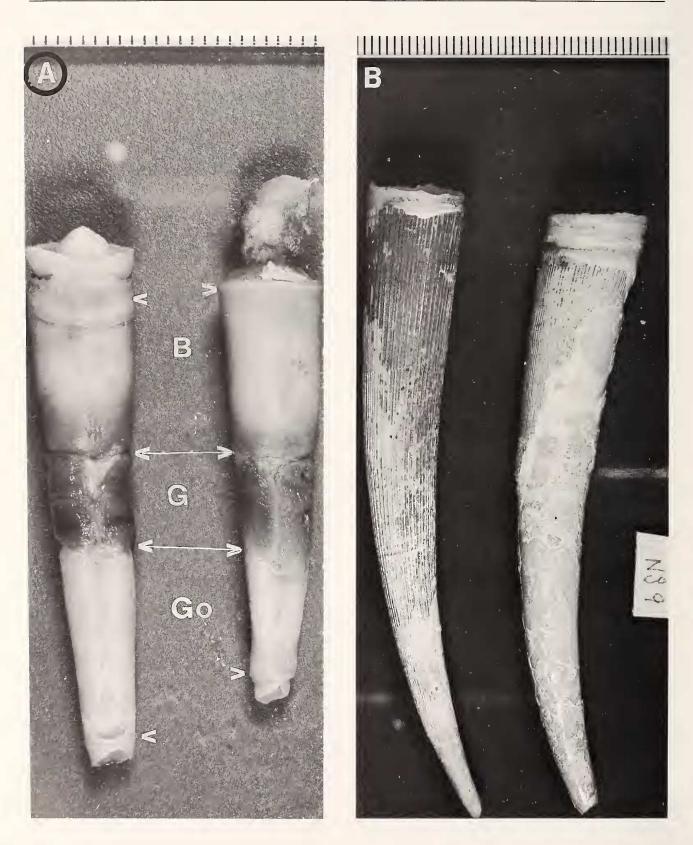
Fissidentalium megathyris was described from Galapagos Island specimens. We did a discriminant analysis classification for the factor of collection location to verify that the Californian F. megathyris specimens we used for comparisons were indistinguishable from the Galapagos type specimens. This analysis was based on the data variables of total length (LTot), length to maximum arc (Larc), aperture width (ApW), and aperture height (ApH). For this analysis we used the 56 California F. megathyris specimens from the Moss Landing Marine Laboratories collection (Lots P3, M4, and LIIT14), the United States National Museum collection (Lots 265901, 266823), and the California Academy of Sciences (Lot 085479) (Table 1). One specimen from the Moss Landing Marine Laboratories collection could not be measured because of shell fractures. These California specimens were compared with the two specimens collected from the Galapagos with label designations as the "lectotype" and the "figured type" (from USNM lots 594262 and 95851 respectively). Although the two Galapagos specimens were, on the average, larger than the California specimens, the calculated  $\chi^2$ probability that these specimens could be drawn from the same population was 0.14. Consequently, the specimens from California designated as F. megathyris could not be statistically distinguished, with an  $\alpha$  probability of < 0.05, from those specimens designated as the *F. megathyris* lectotype or figured type.

## Soft-Body-Part Measurements

Soft-body-part proportions were measured from fixed material, which has been shown to provide reliable quantitative data (Figure 2A) (Voight, 1991). Three basic softbody-part components were measured. The first was the bucco-pedal region, for brevity referred to here as the buccal region, measured ventrally from the so-called periostracal groove on the outside of the mantle surrounding the ventral aperture to the groove separating this ventral component from the remaining soft body parts. This groove is formed in the region of the bifurcation of the mantle sinus and may be a fixation artifact (Steiner, personal communication). Nevertheless, it was a consistent landmark. The second was the gut region, measured ventrally from the groove separating the gut area from the buccal region to the position of the anus. The third was the gonadal region. This was measured ventrally from the anus to the mantle attachment ring on the mantle surrounding the dorsal aperture, and dorsally from the most posterior margin of the stomach to the mantle attachment ring surrounding the dorsal aperture.

## **Radular Morphometrics**

Whole radulae were dissected from preserved animals, and teeth separated prior to measuring. The following



measurements were taken: rachidian tooth width (RW) and length (RL); lateral tooth height (LH) and width (LW); and marginal tooth height (MH) and three width measurements, upper (MUW), middle (MMW), and lower (MLW) (Figures 3, 4, 5). All measurements were made using an image analysis system (Image 1.2 for Macintosh) through an Olympus SZ40 dissecting microscope.

Five animals of each type and six rows/animal (one tooth of each type/row) were measured for 30 measurements/axis/type. All measurements were compared using the Mann-Whitney U test.

## Scanning Electron Microscopy

Measurements were made from whole radulae and individual teeth which were hand-cleaned with forceps and water, cleaned of tissue residue in 5% sodium hypochlorite, and ultrasonically treated. They were then dehydrated to 100 percent ethanol, air dried, mounted with silver paint on aluminum stubs, and gold plated. Micrographs were taken with an ISI SX 30 Scanning Electron Microscope (SEM) at 14 KeV. Additional samples for subsequent examination were examined with a JEOL JCS-100 at 20 KeV.

## Shell Microstructure

Shells were either hand-broken or cut with a Buehler Isomet (diamond blade) saw in cross section and longitudinally. Some shells were etched in a 5% sodium hypochlorite solution to allow for more distinct differentiation of the various layers. All shells were viewed with an SEM with preparations as indicated above. Surveys of shell edges, inside, and outside surfaces were conducted. Due to shell erosion, numerous shells and locations had to be examined to describe the number and type of layers.

#### Statistics

The means and standard errors of the measurements or the derived indices were computed, except for the whorl expansion rate (Ws). The whorl expansion rate is a logarithmic function, and calculations of this index are sensitive to small changes of shape. We used the mean of the natural logarithm of this index for comparative purposes. The mean of a logarithmically transformed numerical array is the median of the untransformed array. The median is a better indicator of the central tendency of that array than the mean, as it is less sensitive to extreme values (Sokal & Rohlf, 1981). The mean Ws is also given for comparative purposes.

The morphometric factors and indices were compared between and within populations by using standard statistical graphics software (Manugistics, 1992). When small samples were compared or when the assumptions inherent in parametric tests could not be met, distribution-free or non-parametric tests (such as the Mann-Whitney U) were used, even though they were less powerful. The data were examined between the species with regard to homogeneity of variance using Cochran's and Bartlett's tests. Similarly, all data were tested with a Kolomogorov test for their fit to a normal distribution. Parametric tests, such as Analysis of Variance, were only used when the inherent assumptions of normality and homogeneity of variance could be met (Zar, 1984).

With the exception of the whorl expansion rate, all of the data sets showed non-significant differences in variance and were not significantly different from a normal distribution. Because the conditions of normality and homogeneity of variance could be met, the data were examined using a one-way Analysis of Variance for each of the measured factors. The proportional data were arc-sin transformed prior to these analyses.

We used five basic measurements and nine calculated values to describe the shell (Tables 2, 3). Throughout this study, statistical significance was defined as  $P = \alpha \le 0.05$ .

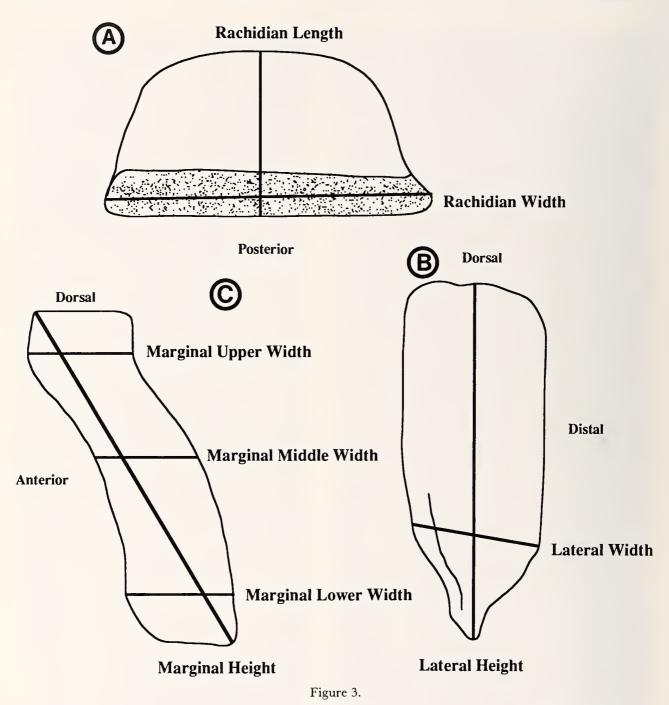
## Tabular Data Appendix

The numerous morphometric comparisons and statistical procedures used in this study generate large amounts of tabular data that are necessary for the analyses leading to the species description. Nonetheless, many of those data are superfluous to the actual species description, and are expensive to publish. All of the statistically significant differences determined from the comparisons are summarized in Table 4. All of the comparisons of differences, including both statistically significant and insignificant data, are grouped in the following tables in an electronically available data appendix.

Appendix Table 1. Summary of meristic factors for *Fissidentalium megathyris* and *F. erosum.* 

#### Figure 2.

Soft body parts and shells of California Fissidentalium erosum Shimek & Moreno, sp. nov. and F. megathyris collected from MLML Station P3. A. Left: Soft body parts from F. megathyris (Specimen FM-7), Right: Soft body parts from F. erosum Shimek & Moreno, sp. nov. (Specimen NS-16). Arrowheads indicate measuring points. B = Bucco-pedal region, G = Gut region, Go = Gonadal region. B. Left: Shell from F. megathyris (Specimen FM-20), Right: Shell from F. erosum Shimek & Moreno, sp. nov. (Specimen NS-9; LACM # 2755). Scale bar is in millimeters.



A. Dorsal view of a typical rachidian tooth. Measurements taken were Rachidian Length (RL) and Rachidian Width (RW). B. Anterior view of a typical lateral tooth. Measurements taken were Lateral Length (LH) and Lateral Width (LW) of the tooth at the tooth "handle" (See Figure 4A). C. Distal view of a typical marginal tooth. Measurements taken were Marginal Height (MH), Marginal Upper Width (MUW), Marginal Middle Width (MMW), and Marginal Lower Width (MLW). MUW and MLW were taken at the curvatures of the teeth.

Appendix Table 2. Results of two factor comparisons of soft body part length measurements of *Fissidental-ium megathyris* and *F. erosum* using the Mann-Whitney U test.

Appendix Table 3. Results of One-way ANOVAs testing factor differences by species for *F. megathyris* and *F. erosum*.

Appendix Table 4. Results of two-sample compari-

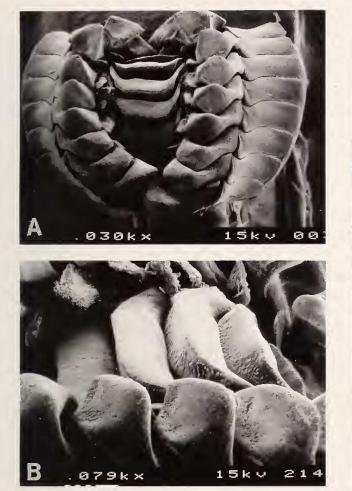


Figure 4.

Radula of *Fissidentalium erosum* Shimek & Moreno, sp. nov. Specimen NS-3. A. Whole radula. Figures 4B, 5A and 5B are oblique views from the right side of this preparation. B. Lateral view of rachidian and heads of lateral teeth.

sons made with a Mann-Whitney U test for the measurement indicated.

These data may be useful for other comparative taxonomic work, and are available electronically by anonymous FTP from ucmp1.berkeley.edu.

# SYSTEMATICS

Class Scaphopoda Bronn, 1862

Order Dentaliida Da Costa, 1776

Family DENTALIIDAE Gray, 1834

Fissidentalium P. Fischer, 1885

Type species: Dentalium ergasticum P. Fisher, 1882 (designation by monotypy).

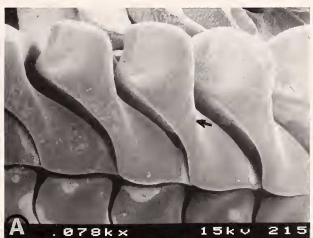




Figure 5.

Radula of *Fissidentalium erosum* Shimek & Moreno, sp. nov. Specimen NS-3. A. Dorso-lateral (oblique) view of the lateral teeth. Arrow indicates "tooth handle". B. Dorso-lateral oblique view of the marginal teeth.

Fissidentalium contains numerous large, deep-water species. The shells are robust, and generally possess many longitudinal ribs or striae. The generic name refers to the presence of a narrow posterior (on the convex side) slit proceeding ventrally from the dorsal aperture (Emerson, 1962; Palmer, 1974b; Steiner, 1992). This slit is found in many Fissidentalium species, but is lacking in a few, notably F. megathyris. Fissidentalium is easily recognized and widespread; however, most of the species have been described on the basis of limited collections and are relatively similar in gross morphology (Pilsbry & Sharp 1897; Palmer 1974a).

> Fissidentalium erosum Shimek & Moreno, sp. nov.

Type Material: Holotype: LACM # 2755 (Figure 1B);

# Table 2

Basic measurem	ents
LTot	= Total length
Larc	<ul> <li>Length from the posterior aperture forward to the point of maximum distance to the shell from a chord running between the dorsal edges of both apertures.</li> </ul>
ApW	= Aperture width
ApH	= Aperture height
arc	= Maximum distance to the shell from a chord running between the dorsal edges of both apertures.
Derived indices	
lnLtot	= Natural logarithm of (LTot)
lnLarc	= Natural logarithm of (Larc)
lnApW1	= Natural logarithm of $((ApW) + 1)$
lnApH1	= Natural logarithm of $((ApH) + 1)$
lnŴmax1	= Natural logarithm of $((Wmax) + 1)$
Lindex	= Natural logarithm of $((LWmax) + 1)/natural logarithm of (LTot)$
whratio	= (ApW)/(ApH)
Apratio	= Natural logarithm of $((ApW) + 1)/natural logarithm of ((ApH) + 1)$
Ws	$=\frac{LTot}{\sqrt{(LTot - Larc)^2 + (\operatorname{arc})^2}} \overline{\frac{1}{\operatorname{atan}\left(\frac{(\operatorname{arc})}{LTot - Larc}\right)}}$

Shell measurements taken of F. megathyris and F. erosum. See Figure 1.

Paratypes: LACM # 2756, USNM # 880041, BMNH # 199405.

**Type locality:** Station P3 (Moss Landing Marine Laboratories Designation), Pioneer Canyon, off Central California. Collected with a beam trawl at 37°03.27'N, 123°26.30'W (trawl on bottom) to 37°03.97'N, 123°25.26'W (trawl off bottom), on 29 February 1992, at depths ranging from 3090 m to 3300 m.

Material examined: We examined 19 specimens of Fissidentalium erosum. The same number of F. megathyris

# Table 3

Type specimen measurements. Specimen BMNH 199405 had a fractured shell; consequently no shell measurements are listed. All measurements are in millimeters. Measurements and derivations are described in Table 2 and Figure 1.

Category	Holotype	Paratype	Paratype	Paratype	Paratype	Paratype
Museum	LACM	USNM	LACM	USNM	BMNH	BMNH
Lot Number	2755	880041	2756	880041	199405	199405
A. Shell Measurements						
LTot	77.8	72.2	74.2	76.0		62.2
Larc	36.6	28.9	36.1	39.1		28.0
ApW	11.9	11.5	12.7	11.8		11.3
ApH	11.9	11.4	12.5	12.0		11.2
arc	5.1	2.9	6.4	5.4		5.2
<b>B.</b> Derived Indices						
lnLtot	4.4	4.3	4.3	4.3		4.1
lnLarc	3.6	3.4	3.6	3.7		3.3
lnApW1	2.6	2.5	2.6	2.5		2.5
lnApH1	2.6	2.5	2.6	2.6		2.5
Apratio	1.0	1.0	1.0	1.0		1.0
Ŵs	167.1	2244.0	50.6	133.1		49.7
whratio	1.0	1.0	1.0	1.0		1.0
C. Soft Body Part Lengt	h Measurements					
Total soft body parts	38.9	30.0	33.8	35.1	31.2	33.9
Buccal region	12.1	15.4	14.9	17.0	12.0	15.6
Gut region	9.6	4.3	6.1	5.6	8.3	7.8
Gonadal regions						
(Ventral)	17.2	10.3	12.8	12.5	10.9	10.5
(Dorsal)	16.7	11.4	15.0	11.7	13.0	14.6

# Table 4

Significantly different characteristics and the test determining their differences. P = probability that the characteristic values in the *F. megathyris* and *F. erosum* are drawn from the same population. \* = Proportions were Arc-Sin transformed prior to the ANOVA.

Characteristic	P	Test
Shell Characteristics		
LTot	< 0.001	ANOVA
lnLtot	< 0.001	ANOVA
Apratio	< 0.01	Mann-Whitney U
ApW/ApH	< 0.01	Mann-Whitney U
Soft Body Part Characteristics		
Total soft body part length	< 0.01	Mann-Whitney U
Total soft body parts length	< 0.001	ANOVA
Gut region length	0.05	Mann-Whitney U
Gonadal region, dorsal length	< 0.01	Mann-Whitney U
Gonadal region, dorsal length	< 0.001	ANOVA
Gonadal region, ventral length	< 0.01	Mann-Whitney U
Gonadal region, ventral length	< 0.001	ANOVA
Proportion of Total Soft Body Part Length	s	
Buccal region length	< 0.01	Mann-Whitney U
Buccal region length	0.001	ANOVA*
Gonadal region, ventral length	< 0.01	Mann-Whitney U
Gonadal region, ventral length	< 0.01	ANOVA*
Radular Tooth Characteristics		
Rachidian tooth width	0.012	Mann-Whitney U
Lateral tooth width	0.036	Mann-Whitney U
Marginal tooth height	0.012	Mann-Whitney U
Marginal tooth middle width	0.033	Mann-Whitney U
Marginal tooth lower width	0.020	Mann-Whitney U

was also collected from the site. Additional museum lots of *F. megathyris* specimens, including the type material, were examined for comparative purposes (Tables 1, 3).

**Etymology:** The epithet *erosum* refers to the shell erosion that characterizes this species.

**Diagnosis:** Shell large, over 65 mm long and 13 mm in ventral aperture diameter, evenly curved, point of maximum curvature posterior to, but near, shell middle. Outer shell layers, particularly near the dorsal aperture, eroded. Shell white, often with adherent black material. Ventral aperture oblique, slightly wider than high. Preserved, unrelaxed, soft-body-part mass divisible into the buccal (ventral), gut (middle), and gonadal (dorsal) portions and less than half total shell length; buccal and gonadal lengths approximately equal and each about 2/5 of total length.

**Detailed description:** Specific measurements of the holotype and paratypes are given in Table 3. Unless otherwise noted, all measurements in the description are means  $\pm$  one standard error of all *F. erosum* specimens and were taken from Appendix Table 1.

Shell large, mean total shell length  $69.20 \pm 1.40$  mm, evenly curved; shell length from dorsal aperture to point of maximum curvature  $31.67 \pm 1.17$  mm; point of maximum arc posterior to, but near, the shell middle (Figure 2B).

Ventral aperture slightly oblique to dorso-ventral axis; approximately circular; aperture width  $11.89 \pm 0.15$  mm; aperture height  $11.74 \pm 0.15$  mm. Although not significantly different, most ventral apertures are wider than high.

Shell curvature moderate; maximum curvature  $4.43 \pm 0.33$  mm; whorl expansion rate  $615 \pm 284$ .

Length of preserved, unrelaxed, soft-body-part mass  $31.42 \pm 1.10$  mm; length of buccal region  $14.32 \pm 0.57$  mm; gut region  $6.96 \pm 0.39$  mm. Ventral gonadal region length  $10.14 \pm 0.61$  mm; dorsal gonadal region length  $12.23 \pm 0.49$  mm.

Radula of "Antalis type" (Chistikov 1975); lateral teeth convex anteriorly and concave posteriorly with sharply pointed forward projections where bent (Figures 3B and 4A); marginal teeth with wavy contours and three curvatures (Figure 4B), rachidian teeth concave dorsally, with transverse ridges, and "S"-shaped, allowing the teeth to fit tightly together (Figure 4B). Rachidian and lateral teeth movable on radular ribbon; marginal teeth immobile, imbedded in ribbon.

Radular tooth measurements were from five animals slightly smaller than sample mean size; aperture width  $11.62 \pm 0.20$  mm., aperture height  $11.42 \pm 0.15$  mm. Rachidian tooth length  $61.00 \pm 1.10 \ \mu$ m, width  $100.8 \pm 1.28 \ \mu$ m; lateral tooth height  $105.6 \pm 1.20 \ \mu$ m, width 53.2



## Figure 6.

Fissidentalium megathyris. Specimen F from USNM lot 95851, labeled paratypes, figured types. Scale bar is in millimeters.

 $\pm$  1.77 µm; marginal tooth height 118.2  $\pm$  3.84 µm, top width 37.8  $\pm$  1.93 µm, middle width 33.6  $\pm$  1.69 µm, lower edge width 35.0  $\pm$  1.38 µm.

Shell with three layers; ribbed outer aprismatic layer, partially or completely eroded particularly near dorsal aperture, 20-40  $\mu$ m thick; middle prismastic layer, 750  $\mu$ m thick; inner aprismatic layer, 50  $\mu$ m thick.

Shell white, adherent black material found on some specimens. Shell dorsal apical end often missing, due to decollation (Reynolds, 1992) or predation (Shimek, 1990).

**Remarks:** All of the *F. erosum* examined were adults, although a few small *F. megathyris* shells were examined during the comparisons. No *F. erosum* juveniles were collected, probably due to the sampling method. The gender of all the animals was not determined when the animals were measured, but an examination of eight haphazardly selected individuals indicated three males, four females, and one whose gender was indeterminate due to poor preservation; consequently the differences between *F. erosum* and *F. megathyris* were not likely due to sexual characteristics. Gametes filled each gonad; the animals gave no appearance of having recently spawned.

Fissidentalium erosum was externally similar in most regards to F. megathyris (Figures 2B, 6), and could easily be confused with it. The major differences were the amount of erosion, and the dorsoventrally flattened ventral aperture. We attempted to determine if the erosional difference was due to some structural difference in the shell. No significant differences were apparent; however, the F. erosum shells were too eroded to draw definitive conclusions.

We compared shell, soft-body-part, and radular meristic characters to determine if the two morphologies were actually statistically distinct species. On the basis of shells alone, these two morphologies were statistically distinct only as regards the ratios of the ventral aperture width to aperture height (Table 4, Appendix Table 1), as examined with the nonparametric tests. Using the Mann-Whitney U test, both the untransformed and the logarithmically transformed aperture ratios were different between the two species; *Fissidentalium erosum* apertures were significantly wider for a given height than were the ventral apertures of *F. megathyris* (Apratio, Z = -3.536, probability of ratios being different < 0.01; ApW/ApH, Z = -3.602, probability of ratios being different < 0.01).

On the basis of gross soft-body-part morphology, the species were more clearly distinct (Table 4, Appendix Tables 1, 2, Figure 2). The total soft body part length was significantly shorter for F. *erosum* than for F. *megathyris*. This difference was largely due to significant differences in the lengths of the gut and gonadal lobes. The buccal region was a significantly greater proportion of the total soft body parts in F. *erosum* than in F. *megathyris*, while the gut and the dorsal measurements of gonadal lobes were not proportionally different in size. The ventral measurement of the gonadal region was proportionally larger in F. *megathyris* than in F. *megathyris* than in F. *megathyris* than in F.

Of the untransformed or transformed shell parameters, only total length was statistically significantly different between the two species (Table 4, Appendix Table 3). As the apertural measurements were not statistically different, this indicates that *F. megathyris* is longer for a given aperture measurement than is *F. erosum*.

The total soft-body-part lengths were significantly different utilizing the one-way analysis of variance. This significant difference was due primarily to the differences in the length of the gonadal region, which was larger in *F. megathyris*. The dorsal and ventral gonadal region proportions of the soft body part components were statistically significantly different between the two species, utilizing this test as well (Table 4, Appendix Table 3).

We interpreted these data to indicate that *F. erosum* individuals were "stubbier" than those of *F. megathyris*, being shorter for a given width. This subtle truncation in length was reflected in the soft body part anatomy, where the gonadal component of the soft body parts was confined in a smaller space in *F. erosum*. The middle or gut region, which contained the radula and radular musculature, was not different between the two species, possibly indicating a similar food.

Examination of radular characteristics from paired animals showed significant differences as well. These data were too few to be sure that the assumptions for an analysis of variance could be met, so the comparisons were made utilizing the non-parametric Mann-Whitney U test. The animals were chosen to provide as close a match as we could get between the paired animals. The aperture widths were not significantly different. As expected however, the aperture heights were significantly different (Table 4, Appendix Table 4). The rachidian and lateral teeth were significantly wider in F. megathyris than in F. erosum, although the heights were not significantly different. Most of the marginal tooth measurements were significantly different between the two species; only the upper marginal tooth width was not significantly different. In all significantly different cases, the F. megathyris radular teeth were larger or more robust.

The significant differences between these two morphologies were related to both relative and proportional differences in size, and were reflected in both internal and some external meristic factors (Table 4). Additionally, there were radular differences, possibly reflecting differences in either prey eaten, or the method of eating it. Finally some of the more qualitative shell morphological differences, such as the amount of shell erosion, may indicate differential habitat utilizations. Because of all of these differences, we concluded that the two morphologies were from two distinct species: the larger, more elongate *F. megathyris*, and the smaller, stubbier *F. erosum*.

# ACKNOWLEDGMENTS

We thank the skippers and crews of the R/V Point Sur and R/V Wecoma for their support in the sampling phase of this project. Many thanks are also due to the staff and students from the Moss Landing Marine Laboratories (MLML) who participated in the collecting cruises. We particularly thank Dr. James Nybakken for his assistance during this study. We also thank MLML and PRC Environmental Management for allowing us access to their collections. This project was partially funded by the Navy CLEAN Contract No. N62474-88-D-5086.

We thank Drs. M. G. Harasewych and A. Kabat, National Museum of Natural History, T. Gosliner, California Academy of Sciences, and J. H. McLean, Los Angeles County Natural History Museum, and their staffs for the loan of comparative material.

We thank J. Blixt of the Veterinary Molecular Biology Laboratory at Montana State University for assistance and the use of SEM facilities, and Dr. Alan Kohn, University of Washington, for research facilities for a portion of this study.

We thank Dr. Gerhard Steiner of the University of Vienna, and Dr. Barry Roth of the University of California for their critical reviews of the manuscript and numerous helpful suggestions.

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